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A new twist in the evolution of chameleons uncovers an extremely specialized optic nerve morphology

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Chameleons are unique among lizards for their exceptional suite of anatomical modifications which has allowed them to adapt to and diversify in arboreal environments. Specializations shared by members of this lineage include a trunk with a reduced number of presacral vertebrae, a body that can be mediolaterally compressed or expanded, reduced flexibility in the trunk and neck, grasping hands and feet, a prehensile and non-autotomizing tail, highly developed and independently movable eyes, and a ballistic tongue. Here we use contrast enhanced computed tomography to describe the arrangement of optic nerves of chameleons and compare them with those of other squamates. Results from dissection and 3D modeling of the brain and associated structures reveal that, in comparison with other squamates (and across tetrapods in general), chameleons have evolved a longer, coiled optic nerve that is likely to provide "slack" to reduce tension on the optic nerve during the extensive rotations characteristic of the chameleon eye. Despite significant study on the visual system of chameleons, our use of non-destructive CT in examining neural cranial anatomy of whole specimens has revealed a previously unreported adaptation that is part of an interconnected suite of features that chameleons have evolved in conjunction with life in a complex three-dimensional arboreal environment.

One third of all lizard species are at least partially arboreal[1]. The transition from two-dimensional terrestrial environments to three-dimensional arboreal habitats has precipitated some remarkable morphological adaptations in squamates, including the sticky toepads of geckos and anoles, the patagia-bearing ribs of gliding *Draco*, and the prehensile tails of Solomon Island skinks (*Corucia*) and arboreal alligator lizards (*Abronia*). Among squamates, no lineage has committed to a tree-dwelling, ambush foraging lifestyle more completely than chameleons, which have evolved a bewildering combination of apomorphies associated with arboreality. Since splitting with their sister family, the Agamidae, 125 million years ago, chameleons have evolved prehensile tails, grasping hands and feet, rapid color-changing skin, ballistic tongues, deep, laterally compressed bodies, distinctive limb posture, and large, independently movable eyes[2] (Fig. 1). Indeed, their highly specialized and distinctive phenotype (Fig. 1) was considered so fundamentally different from other lizards[3,4] that chameleons were placed in the infraorder Rhiptoglossa[5], separate from all other lizards. Currently, chameleons are classified in the lizard clade Iguania[6] (Fig. 2). Many of these adaptations appear to be associated with chameleons' unique "cruise foraging" behavior, which has been described as an intermediate strategy between active and sit-and-wait foraging[7]. Chameleons rely on ballistic tongue feeding to capture prey at a distances up to 2.5 body lengths away, especially in small species[8]. Their tongue muscles and hyoid skeleton (Fig. 1) are capable of protrusion that is both rapid and extensive[9,10] and is one of the fastest tongues in animal kingdom. Conversely, chameleon limb and body movements are generally slow during prey capture, while their independently mobile eyes have a wide range of movement and allow the head to remain still during prey acquisition.

The eyes of chameleons are proportionally large when compared with other diurnal squamates, with retinal image enlargement and the unique capacity to determine target distance by accommodation cues[11,12]. Some chameleon species such as *Chamaeleo dilepis* possess a unique specialization related to a crystalline lens (Fig. 1) with negative refracting power when compared with other vertebrates[12]. When chameleons scan the environment searching for prey or potential predators, their eyes move independently in all directions[3,13–16].

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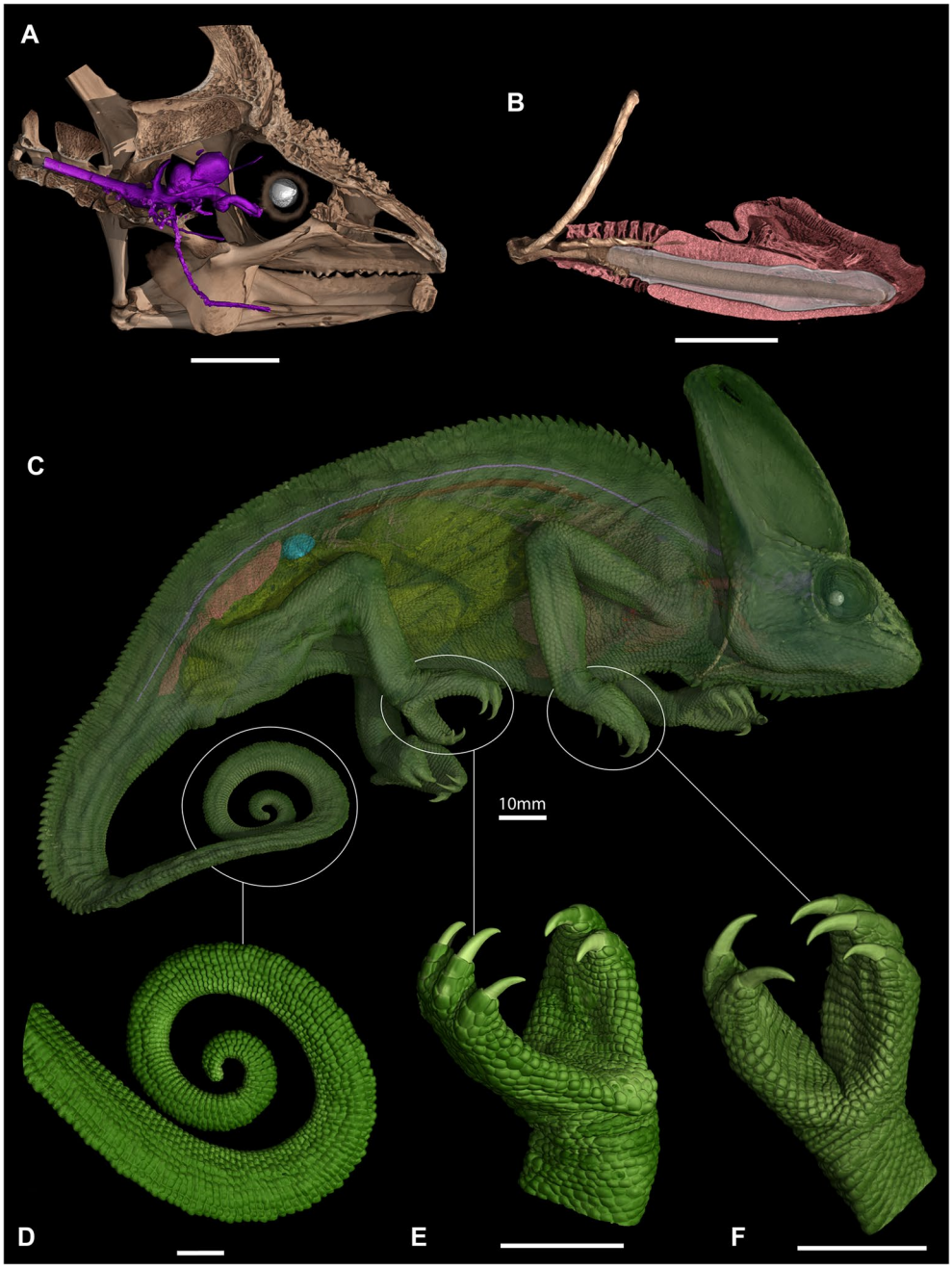

Fig. 1. Three-dimensional rendering of *Chamaeleo calyptratus* Chamaeleonidae (UF: Herp: 191369). (**A**) Skull with brain and optic nerve in situ; (**B**) Retracted tongue with hyoid apparatus; (**C**) Lateral view of a whole specimen showing the spinal cord, parts of the circulatory and urogenital system; (**D**) Distal portion of the prehensile tail; (**E**) Right foot; (**F**) Right hand.

Independent eye movement has also evolved in invertebrates such as mantis shrimp and other crustaceans[17,18] and, among vertebrates, in several groups of teleost fishes[16,19], Great-Tailed Grackles (*Quiscalus mexicanus*)[20], and in some anoles (e.g. *Anolis cuvieri, A. occultus*, and the Cuban "*Chamaeleolis*" *Anolis* group)[21–23].

Eye movement in chameleons is best regarded as context dependent rather than strictly independent because eye movements are coordinated and decoupled during scanning but conjugate during binocular tracking[12,24,25]. The brain of chameleons has been studied in detail[26–28], including the anatomy and development of cranial nerves[29,30]. One main modification of the chameleon brain, that also applies to iguanians in general, is the reduction of the complexity the olfactory lobes (Fig. 2). Prior anatomical work has demonstrated that chameleons have a prominent optic chiasm[26,31], and this has been correlated with their wide range of eye movements[2,28].

With such highly mobile eyes, the optic nerves of chameleons may also be expected to display compensatory modifications such as slack, which accommodate the strain caused by tensile forces as has been reported in

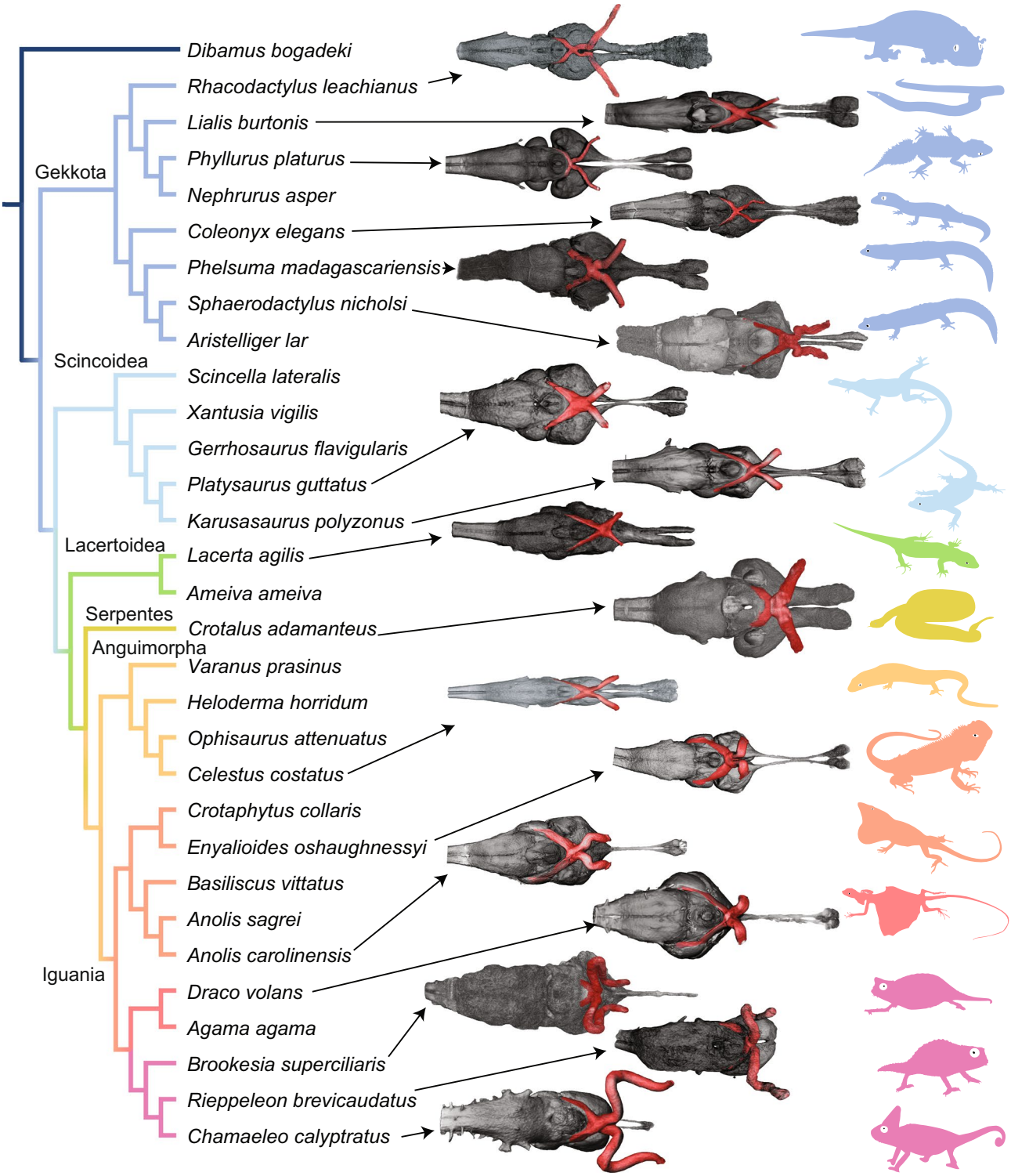

Fig. 2. Phylogenetic relationships and three-dimensional renderings of the brains of 17 squamate reptiles, representing the main high order groups. Some of the taxa examined includes a ventral view of the brain with the optic nerves highlighted in red and a reference silhouette.

rodents and humans[32]. In rodents, it has been reported that the optic nerve axons (and others in the peripheral nervous system) have wavy fibers that permit a degree of stretching during movement[32,33].

In this paper we revisit previously published work on chameleon optic anatomy, encompassing more than 2000 years of observations, including considerations by authors such as Aristotle[34] and Newton[35], early modern period anatomists[36–39], and recent observations based on modern dissections and digital imaging techniques[27,31,40,41]. Despite extensive past consideration of chameleon eyes, the unique in-situ arrangement

of chameleon optic nerves, which is often lost with physical dissections, has not been described. In this paper we use contrast enhanced computed tomography to explore the three-dimensional tissue morphology of the optic nerve in chameleons relative to other squamates and show that the optic nerves of adult chameleons are proportionally long and have a unique coiled path. This morphology is developed early during ontogeny and is accomplished through changes observed in three embryonic stages. Finally, we propose a model based on functionally correlated traits that can be used to infer the sequence of morphological changes in the chameleon Bauplan.

Results

We studied adult specimens of 34 squamates species, using contrast enhanced computed tomography. 3D models of the brain and the optic nerve for 17 species were plotted onto a phylogenetic tree. The three chamaeleonid taxa included in this study represent highly divergent lineages and vary in adult body size (*Brookesia superciliaris*, SVL 46–54 mm; *Rieppeleon brevicaudatus*, 80 mm; and *Chamaeleo calyptratus*, 300 mm) and ecology: *Brookesia* and *Rieppeleon* are terrestrial or climb on low vegetation whereas *Chamaeleo* is arboreal.

The optic nerves of all three chameleon species are extensively coiled (Figs. 2, 5A–D), extending anteriorly from the optic chiasm, passing between the orbitosphenoid bones, turning laterally and then anteriorly towards the juncture with the sclera, and containing multiple 90-degree bends along their length. In the adult Veiled Chameleon (*C. calyptratus* Figs. 1, 4–5), the optic nerves meet at a narrow point in the optic chiasm: the first inflection point (Fig. 5, #1) is immediately anterior to the orbitosphenoids whence the tracts diverge posterolaterally. The second inflection point (Fig. 5, #2) twists laterodorsally. Relative to the origin on the brain, the right nerve turns counterclockwise, left nerve clockwise. From this point the optic nerves are directed anterodorsally for a short segment until they reach a third inflection point (Fig. 5, #3) where they bend anteroventrally, and end in a short sigmoid segment that terminates at the juncture with the sclera. The path is similar in *Rieppeleon* and *Brookesia*, but in *Rieppeleon* there is a fourth inflection point between the third and the sigmoid segment, and in *Brookesia* the tracks are more coiled, producing one complete loop.

This coiled arrangement results in chameleon optic nerves being much longer than the linear distance between the optic chiasm and the juncture with the sclera (hereafter referred to as length-to-distance ratio—see Fig. 5A–F). The ratio for adult chameleons were: *B. superciliaris* 3.36 (L)—2.25 (R), *R. brevicaudatus* 1.72 (L)—2.33 (R), and *C. calyptratus* 1.89 (L)—1.67 (R). The significantly different contralateral values are likely attributable to the position of the eyes at fixation (Fig. 3). In all other of squamates observed in this study, the optic nerves are straighter, and the length-to-distance ratios are closer to 1 (Fig. 2, Supplementary Table 1). Many iguanian and gekkotan squamates were shown to have more circuitous optic nerves than scincoid, lacertoid, anguimorphan and ophidian species, which all have relatively straight optic nerves (Fig. 2). Anoles and sphaerodactyl geckos are known for using visual cues and increased eye mobility during their social interactions[42–44]. Of the species studied, *Sphaerodactylus nicholsi*, exhibit the highest length-distance ratios, their optic nerves possessing a short, tight, laterally oriented coil just anterior to the optic chiasm (Fig. 2). These geckos are part of clade of the World's smallest amniotes[45,46], and are notably for their binocular vision, capability of rotating their eyes forward, and having well developed and concaviclivate foveae[47].

It is evident from DiceCT reconstructions that chameleons have significantly longer optic nerves than other squamates (Figs. 2, 3). Significant difference in optic nerve to brain length ratio is recovered between chameleons and all other observed squamates ($p < 0.0001$), and chameleons and other squamates with long optic nerves such as *S. nicholsi*, *A. sagrei,* and *Draco volans* ($p < 0.001$).

We observed lengthening of the optic nerve across three embryonic stages of the veiled chameleon *C. calyptratus* (Fig. 4). At the earliest stage available (100 days post oviposition, dpo), the optic nerves are straight and oriented laterodorsally, at 150 dpo, the optic nerves are oriented mostly lateromedially, and at 200 dpo, near hatchling, the nerves have developed all the loops seen in the adult. Hatchling chameleons are fully capable of turning their eyes, and the twisting of the optic nerves continues until maturation, when the inflection points are more defined (Fig. 4).

Discussion

Historical perspectives

Chameleons have captured the interest of humans for millennia, with ancient depictions on Egyptian artifacts clearly detailing their unique morphology[48]. Chameleon anatomy, based mainly on observations of *C. chamaeleon*, was described in classic early works by Pliny the Elder, Aristotle, Albertus Magnus and Solinus[34,49–51].

One of the earliest printed descriptions and illustrations of chameleon optic nerves was published by the French anatomist Charles Perrault (1628–1703)[36]. In his work, he refuted two previous contentions, (1) the optic nerves were not so short that the brain was directly continuous and connected to the eyes, as Aristotle described them[34], and (2) the optic nerves of chameleons arise separately from the brain, without joining at an optic chiasma, as described by Roman physician Domico Panaroli (1587–1657)[38]. Perrault clearly stated that the optic nerves originate from two eminences of the brain, and after their junction (optic chiasm), they continue as two long filaments measuring eight *lignes* (~ 18 mm) long. In Perrault's illustration, the eyes are depicted in frontal view, including the optic nerves and a portion of the brain (Fig. 5). The optic nerves show a simple arrangement, which includes a basal structure (the brain) from which two optic nerves emerge, and cross (optic chiasm) and continue along a straight path towards the eyes; just anterodorsal to the optic chiasm, and overlying the optic nerves, there is an inverted "V" shaped structure, but is unclear if this is meant to illustrate another nerve (e.g., a branch of the trigeminal nerve) or if it illustrates a twisted or curved optic nerve (Fig. 5E).

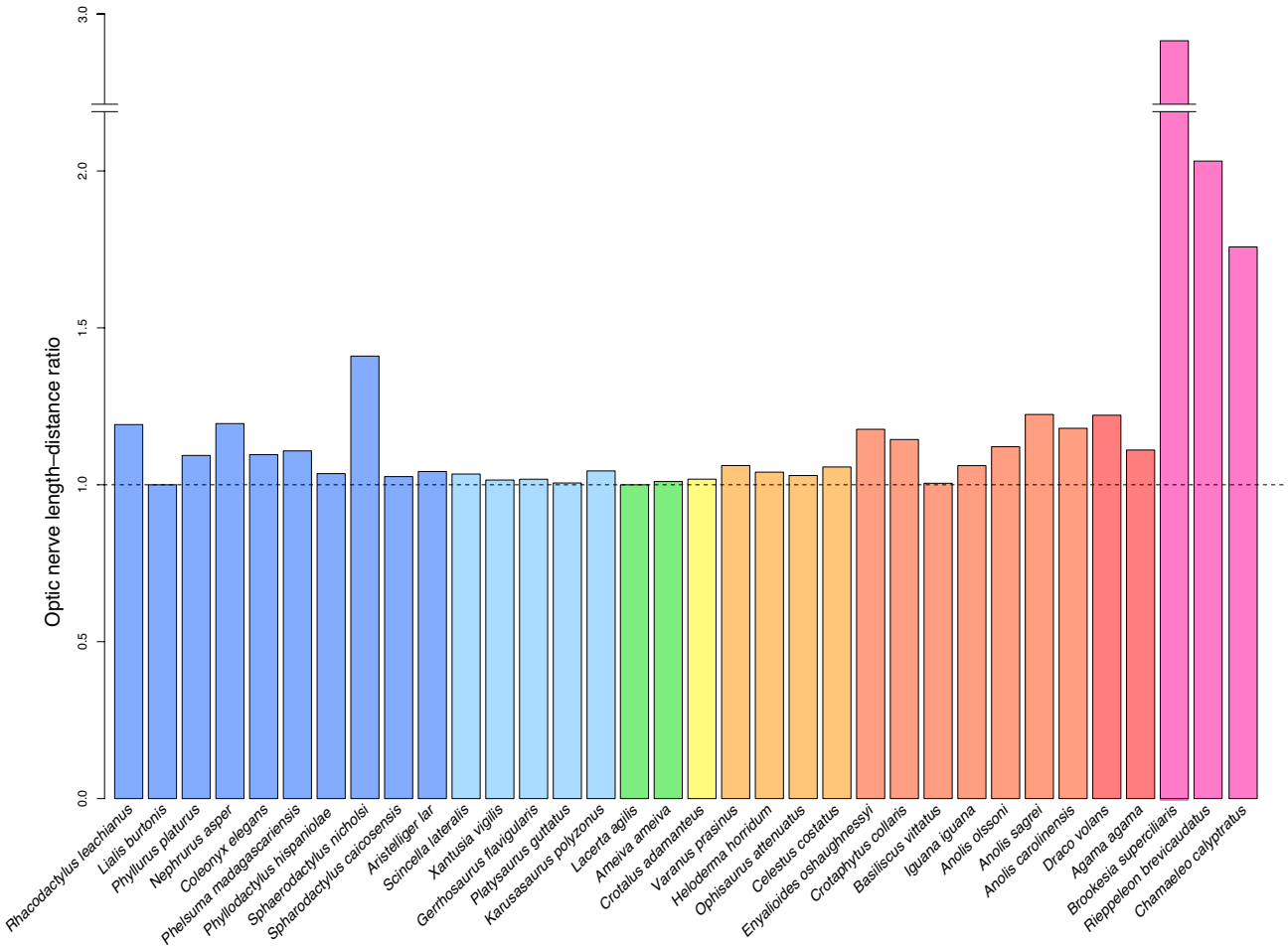

Fig. 3. Average of left and right ratios of optic nerve length to linear distance between the juncture with the sclera and the optic chiasm ratio for all species studied.

Despite this detailed description by Perrault, contemporaneous authors like Newton[35] propagated the interpretation of Panaroli that chameleon optic nerves departed from the brain with scarce contact between them[39] and with no crossing of nerve pathways[37], thus accounting for independent movement of the eyes.

One of the most comprehensive studies of cranial nerves of lizards[29] does not describe in detail the pathway of the optic nerve, only mentioning this structure in reference to the position of a branch of trigeminal nerve: however, the illustration of *C. chamaeleon* in this publication (Fig. 5F) illustrates the proximal segment of the right optic nerve, showing the first inflection point next to the optic chiasm. A photograph of the proximal segment of the chameleon's optic nerve was included in a study[52] of the visual system of *C. chamaeleon*, but the photograph does not show the first inflection point. In more recent studies, the optic nerve of the same species was stained using manganese enhanced MRI[40], and it was noted that the segment from the posterior part of the eye to the optic chiasm (i.e., optic nerve) was "C" shaped. Despite centuries of consideration of the chameleon optic nerves, all previous work has relied on ex-situ examination through dissection, and the coiled pathway of this structure has not been previously documented[11,26,41,52,53]. Our findings add to a growing body of work[54–56] that highlight the benefits of applying microCT approaches to museum collections as a valuable, non-invasive, accessible resource for studying visual ecology.

A new perspective on Chameleon eye movement

The coiled pathway of the optic nerve observed in all three species of adult chameleons (Fig. 2) presumably facilitates increased mobility of the eyes. The slack afforded by this coiling allows extensive rotation of the bulbi oculi without stretching the optic nerve. This unique morphology is also facilitated by the loss of epipterygoid bones in chameleons, which would either constrain the extent to which the optic nerves could be laterally extended, or otherwise would be situated medially to the nerves, and prevent them from straightening when the lizards turn their eyes caudally. Since the three species in this study encompass the most divergent clades of Chamaeleonidae, we infer that extensive coiled optic nerves are a widespread trait in this family. The optic nerves of miniaturized and ground dwelling species (*Brookesia* and *Rieppeleon*) have a higher length-to-distance ratio but are proportionally shorter than the larger, arboreal *Chamaeleo*. A study focused on eye range of motion or optic nerve elasticity using different species of chameleons is needed to understand these morphological

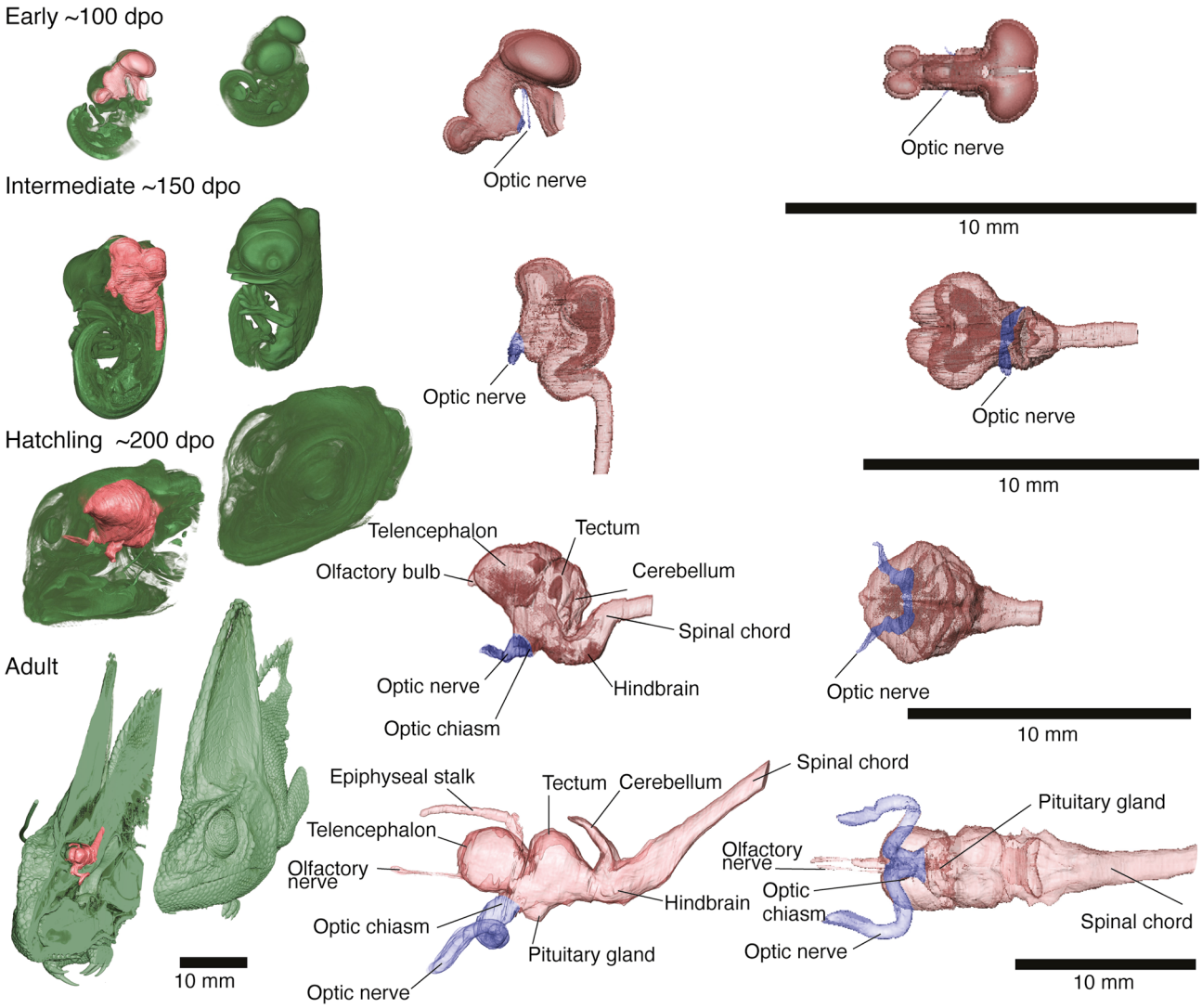

Fig. 4. Development of the optic nerve in the Veiled Chameleon (*Chamaeleo calyptratus*).

differences. To date, the only study of eye rotation in chameleons is examined *Furcifer pardalis*[57], in which horizontal rotation of the eye was calculated to be > 180° and vertical rotation at least 90°: this is still considerably greater than the most mobile eyes among primates (humans), which have 80° and 70° rotations, respectively[58].

Understanding the early morphological transitions leading to the modern chameleon body plan is challenging, since there are no intermediate fossils that indicate the transition from the typical lizard phenotype represented by their sister taxon, the agamid lizards. The oldest chameleon fossils are from the Miocene[59,60], and these already possess many of the group's derived characteristics, and do not offer any clues to the order and timing of the appearance of their specialized traits. Molecular estimates indicate that they diverged from their sister group, the agamids, during the mid to late Cretaceous[6,61–63]. However, some broad associations of morphological traits can be proposed that include the visual system. Among vertebrates with large eyes, there are two contrasting strategies for visual tracking.

Owls and some arboreal mammals (e.g. colugos, lemurs, lorises, galagos and tarsiers), have large eyes with short optic nerves, low eye rotation and high neck rotation. In the former group, the deep orbit in the skull along with a reduction in extraocular muscle size has led to a limit on rotation of the eye muscularly and due to constraints in space for rotation[64–66]. In owls and strepsirrhine primates with "immobile" eyes, a convergent trade off with increased range of motion at the neck has evolved with owls capable of more than 270° rotation in one direction[67].

Chameleons, by contrast, have large eyes, long optic nerves, high eye rotation and low neck mobility. The axial skeleton of chameleons, being shortened and having more vertically oriented zygapophyseal joints in the anterior dorsal region, result in reduced mediolateral (side-to-side) movement and increased stiffness of trunk and neck[68]. Low neck mobility, combined with a mainly motionless posture, might have precipitated the decoupled eye movements and extensive eye rotation, and this association was previously reported in the seventeenth century[69]. Thus chameleons, with their large orbits and extensive capacity for rotation, may benefit from the slack provided by the coiled optic nerve.

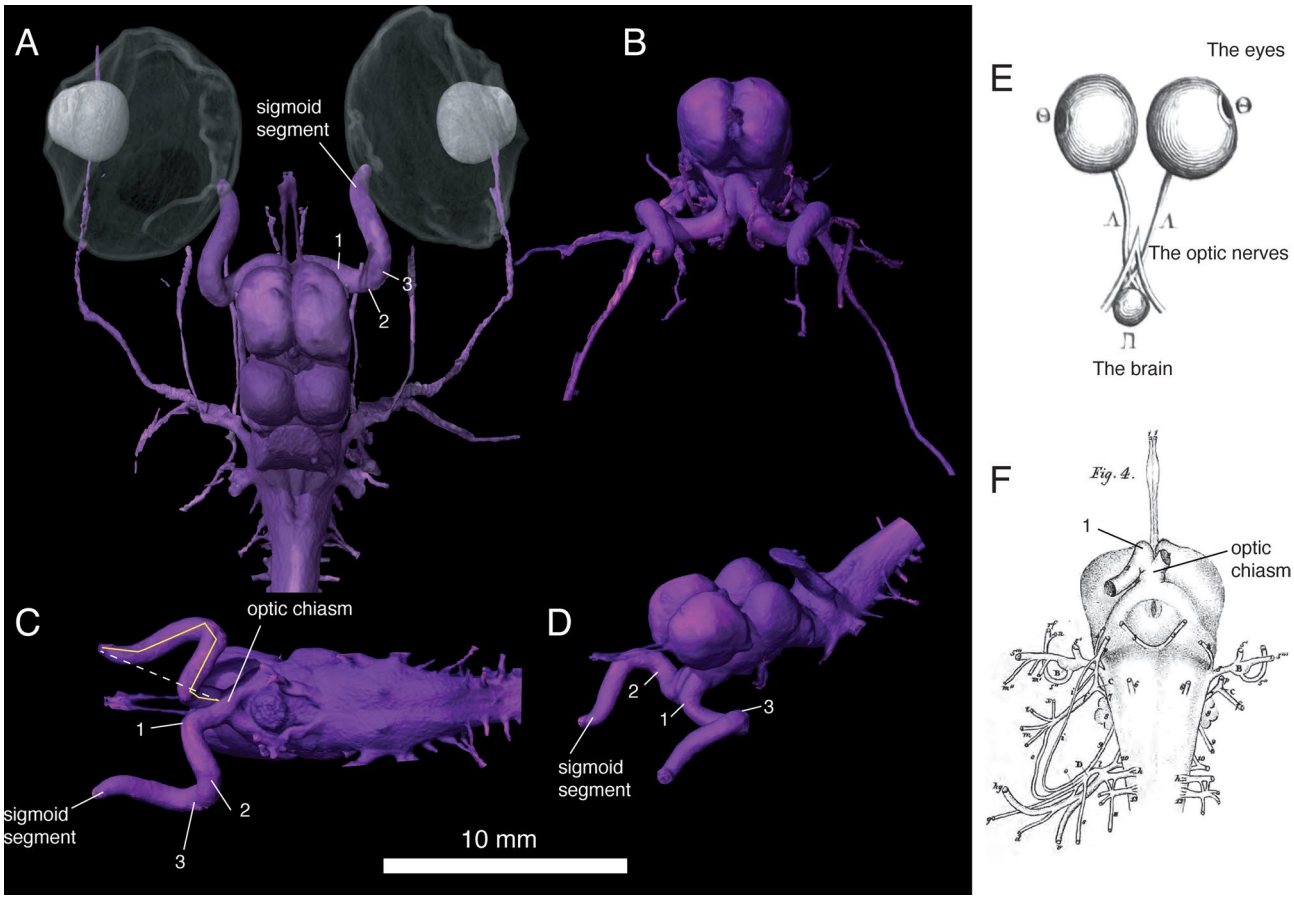

Fig. 5. Details of the inflection points in the optic nerve of the chameleon *Chamaeleo calyptratus* (UF: Herp: 191369). (**A**) Dorsal; (**B**) Anterior; (**C**) Ventral; (**D**) Dorsolateral views. (**C**) Continuous line shows optic nerve length; dotted line shows linear distance. (**E**) Early illustration of the optic nerves of the chameleon by Charles Perrault[36]; (**F**) Brain and origin of cranial nerves of *Chamaeleo chamaeleon* by Johann Gustav Fischer[29]. Scale bar applies only to (**A**–**D**), drawings are not to scale.

Wavy fibers have been identified in the optic nerves of rats[70], which allow the nerves to "stretch", but such fibers have not been found in the chameleon optic nerve[41]. Convoluted optic nerve paths have been described in the larvae of the Ribbon Sawtail Fish (*Idiacanthus fasciola*). The eyes in the larval stage are supported by long stalks with a long optic nerve posterior to the stalk, but as these fish mature, the optic nerve shows gradual retraction and reduction of coiling[71,72]. The occurrence of coiled optic nerves have also been reported among invertebrates; in the Stalk-eye Fly *Cyrtodiopsis whitei* long, coiled optic nerves develop inside the lumen during pupation, allowing for the rapid inflation and elongation of the eye stalks following eclosion[73].

Coiled optic nerves are proposed as an anatomical adaptation that is consistent with increased eye movement of chameleons. We predict that this coiling provides extra slack which decreases strain on the optic nerve and facilitates increased eye rotation. Biomechanical models might help confirm if this adaptation is a response of the optic nerve to reduced physical stress. While this study shows the elongation and coiling of optic nerves to be particularly extreme in Chamaeleonidae, future analysis of optic nerves in other large-eyed, arboreal lizards, including polychrotids and crown giant anoles, may reveal similar neurological adaptations.

Materials and methods

MicroCT imaging

For studying the optic nerve in squamates, 31 diffusible iodine-based contrast enhanced computed tomography (DiceCT)[74] data sets were used (Supplementary Table 1), predominantly produced by the open vertebrate (oVert) thematic collections network[75]. DiceCT employs buffered Lugol's iodine to increase the density of soft tissues, thereby increasing the X-ray opacity and allowing in situ 3D visualization of the central nervous system, including cranial nerves[76]. Each species is represented by one adult specimen, and prior to the scanning, the specimens were immersed in I2KI, or Lugol's solution, until the solution stained the soft tissue. We also examined embryos of the veiled chameleon (*C. calyptratus*) that were infused in phosphotungstic acid (PTA), approximately representing stages 100, 150 and 200 dpo. Most specimens were stained at the UTCT—University of Texas—High-Resolution X-Ray CT Facility, and from Morphosource (OVert: Open Exploration of Vertebrate Diversity in 3D). Three commercial micro-CT scanners were used to obtain the data: Xradia and NSI scanners

at the University of Texas at Austin, and General Electric Phoenix V|tome|x M 240 at the University of Florida in Gainesville.

Brain models

The tomogram stacks from each specimen were imported into Avizo Lite (Thermo Fisher) or VGstudioMax2025.2 (Volume Graphics GmbH, now part of Hexagon) to generate 3D renderings of the brains of the specimens. Each model included the complete brain, the optic nerve, and a portion of the spinal cord. To facilitate the separation of brain tissue from other surrounding tissue (e.g. muscle, glands, bone) in VGStudioMax, the brain and optic nerves were assigned to separate regions of interest using the drawing, edge refinement and clean ROI tools. In Avizo Lite, the brain was enclosed in a virtual box, followed by inverse selection (to select all materials outside the box). These materials were locked. Consequently, the material inside the virtual box corresponding to the brain was selected using the magic wand, with the option of auto selecting along all slices, and with the same material only option activated. During rendering different values of the threshold were used to include mainly brain tissue. The models were finished using the brush and the masking option.

Dissection

One specimen of *Chamaeleo calyptratus* was inspected to corroborate the gross anatomy of the optic nerve in situ. To minimize the distortion caused by this invasive method, we made two transverse incisions of top part of the rostrum using a Dremel Stylo + Versatile Craft Tool with a small diamond cutting disc. The first cut was made along the prefrontal and the anterior portion of the frontal bone. The second cut was made just anterior to the frontoparietal suture and along the frontal and postorbital. The eyelids were detached from the bone and a section of the roof of the skull removed. This exposed the eyes dorsally and the left eye was pushed slightly laterally until the optic nerve was visible. We did not remove entirely the eye to prevent movement or tearing of the nerve. The dissected specimen was photographed using a high resolution.

Keyence Digital Microscope VHX-7000 series (Supplementary Fig. 1).

Morphometrics

Length measurements were obtained using the Avizo lite 3D measuring tool, and VGStudioMax polyline tool, the optic nerves were measured from the optic chiasm to the juncture with the sclera, following the trajectory of the nerve (Fig. 5C), and a linear distance was also taken between these two points, to estimate the direct distance from the optic chiasm to the eye (Indicated by a dashed line on Fig. 5C). We performed a Mann–Whitney test comparing the ratio between the length of the optic nerve and the linear distance length of chameleons and other squamates, also a Kruskall–Wallis test comparing chameleons with other squamates that also shown long optic nerves (i.e. *Sphaerodactylus nicholsi*, *Draco volans* and *Anolis sagrei*).

Specimen source

MicroCT data were obtained from museum specimens housed in the following collections:

Yale Peabody Museum (YPM Herr), the Florida Museum of Natural History (UF Herp), the California Academy of Sciences (CAS) and Personal Collections of Juan D. Daza, Raul E. Diaz Jr. and Richard Thomas (see supplementary Table 1).

Phylogeny

The tree used to illustrate the distribution of brain and optic nerves configurations (Fig. 2), was generated by selecting the species studied in the available Squamate phylogeny subset from the VertLife website (https://vertlife.org)[77].

Ethics statement

The Institutional Animal Care and Use Committee (IACUC) at La Sierra University (jointly with Loma Linda University's IACUC committee) approved the maintenance, breeding, and embryonic collection of veiled chameleons (*Chamaeleo calyptratus*) used in this study (IACUC #LS01). All animal care and welfare were conducted in accordance with relevant guidelines and regulations.

Embryo collection and processing

Chameleons were housed and bred at La Sierra University following our previously described husbandry and breeding protocol[78]. At select time-points during development, eggs with age matched embryos were refrigerated at 4 °C to anaesthetize the ectothermic embryos for a minimum of 2 h. This procedure was also sufficient for humanely euthanizing embryos in ovo prior to harvesting, although MS-222 (tricaine) was also administered as a secondary method of euthanasia[79]. Embryos were harvested in ice-cold phosphate-buffered saline[80] and fixed in 4% paraformaldehyde at four degrees Celsius for a minimum of 5 days. No in vivo testing or research was performed on veiled chameleons. Preserved embryos were subsequently processed for phosphotungstic acid (PTA[80]) where embryos were subsequently scanned in a Nikon Metrology XT225 ST (settings: 70 kV, 130 uA, 1000 ms timing, 1440 projections) a GE Nanotom Phoenix M (settings: 70 kV, 120 uA, 2 averages, 750 ms timing, 1440 projections).

ARRIVE guidelines

The research conforms to the Animals in Research: Reporting In Vivo Experiments (ARRIVE) guidelines.

Data availability

The datasets used and/or analyzed during the current study available from the corresponding author on reasonable request. Additionally, the micro-CT data generated or analyzed in this published article is available to download from MorphoSource (www.morphosource.org).

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References

1. Meiri, S. SquamBase—A database of squamate (Reptilia: Squamata) traits. *Glob. Ecol. Biogeogr.* **33**, e13812. https://doi.org/10.1111/geb.13812 (2024).
2. Anderson, C. & Higham, T. Chameleon anatomy. In *The Biology of Chameleons* (eds. Tolley, K. A. & Herrel, A.) 7–55 (University of California Press, 2014).
3. Owen, C. *An Essay Towards a Natural History of Serpents in Two Parts* (Printed for the author, sold by John Gray, 1746).
4. Laurenti, J. N. *Specimen medicum, exhibens synopsin reptilum emendatam cum experimentis circa venena et antidota reptilum austriacorum*. (Joan. Thom. Nob. de Trattnern Cæs. Reg. Aulæ Typogr. et Bibliop.,1768).
5. Cope, E. D. On the homologies of some of the cranial bones of the Reptilia, and on the systematic arrangement of the class. *Proc. Am. Assoc. Adv. Sci.* **19**, 194–247 (1871).
6. Burbrink, F. T. et al. Interrogating Genomic-scale data for Squamata (Lizards, Snakes, and Amphisbaenians) shows no support for key traditional morphological relationships. *Syst. Biol.* **69**, 502–520 (2019).
7. Butler, M. A. Foraging mode of the chameleon, *Bradypodion pumilum*: A challenge to the sit-and-wait versus active forager paradigm?. *Biol. J. Linn. Soc.* **84**, 797–808 (2005).
8. Anderson, C. V. Off like a shot: scaling of ballistic tongue projection reveals extremely high performance in small chameleons. *Sci. Rep.* **6**, 18625. https://doi.org/10.1038/srep18625 (2016).
9. Herrel, A., Meyers, J. J., Aerts, P. & Nishikawa, K. C. Functional implications of supercontracting muscle in the chameleon tongue retractors. *J. Exp. Biol.* **204**, 3621–3627. https://doi.org/10.1242/jeb.204.21.3621 (2001).
10. Schneider, N. G., Henchal, N. A., Diaz, R. E. Jr. & Anderson, C. V. Feats of supercontractile strength: Functional convergence of supercontracting muscle properties among hyoid musculature in chameleons. *Proc. R. Soc. B.* **292**, 20250078. https://doi.org/10.1098/rspb.2025.0078 (2025).
11. Ketter-Katz, H., Lev-Ari, T. & Katzir, G. Vision in chameleons—A model for non-mammalian vertebrates. *Semin. Cell Dev. Biol.* **106**, 94–105 (2020).
12. Ott, M. & Schaeffel, F. A negatively powered lens in the chameleon. *Nature* **373**, 692–694. https://doi.org/10.1038/373692a0 (1995).
13. Ott, M., Schaeffel, F. & Kirmse, W. Binocular vision and accommodation in prey-catching chameleons. *J. Comp. Physiol. A.* **182**, 319–330 (1998).
14. Lev-Ari, T., Ketter-Katz, H., Lustig, A. & Katzir, G. Visual acuity and optokinetic directionality in the common chameleon (*Chamaeleo chamaeleon*). *EC Ophtalmol.* **6**(5), 145–154 (2017).
15. Paré, A. *Deux livres de chirurgie, I. De la generation de l'homme, et maniere d'extraire les enfans hors du ventre de la mere, ensemble ce qu'il faut faire pour la faire mieux, et plus tost accoucher, avec la cure de plusieurs maladies qui luy peuvent survenir. 2. Des monstres tant terrestres que marins, avec leurs portrait. Plus un petit traité des plaies faites aux parties nerveuses.* (André Wechel, 1573).
16. Pettigrew, D., Collin Shaun, P. & Ott, M. Convergence of specialized behavior, eye movements and visual optics in the sandlance (Teleostei) and the chameleon (Reptilia). *Curr. Biol.* **9**, 421–424 (1999).
17. Land, M. F., Marshall, J. N., Brownless, D. & Cronin, T. W. The eye-movements of the mantis shrimp *Odontodactylus scyllarus* (Crustacea: Stomatopoda). *J. Comp. Physiol. A* **167**, 155–166 (1990).
18. Cronin, T. W. & Porter, M. L. Exceptional variation on a common theme: The evolution of crustacean compound eyes. *Evol. Educ. Outr.* **1**, 463–475. https://doi.org/10.1007/s12052-008-0085-0 (2008).
19. Fritsches, K. & Marshall, N. Independent and conjugate eye movements during optokinesis in teleost fish. *J. Exp. Biol.* **205**, 1241–1252. https://doi.org/10.1242/jeb.205.9.1241 (2002).
20. Yorzinski, J. Great-tailed grackles can independently direct their eyes toward different targets. *Exp. Brain Res.* **239**, 2119–2126 (2021).
21. Thomas, R. A new anole (Sauria: Iguanidae) from Puerto Rico. Part II. Field observations on *Anolis occultus* Williams and Rivero. *Breviora* **231**, 10–18 (1965).
22. Williams, E. E. & Rivero, J. A. A new anole (Sauria: Iguanidae) from Puerto Rico. Part I. Description. *Breviora* **231**, 1–9 (1965).
23. Schwartz, A. & Henderson, R. W. *Amphibians and Reptiles of the West Indies. Descriptions, Distributions and Natural History* (University of Florida Press, 1991).
24. Ketter-Katz, H. et al. Eye movements in chameleons are not truly independent – evidence from simultaneous monocular tracking of two targets. *J. Exp. Biol.* **218**, 2097–2105 (2015).
25. Ott, M. Chameleons have independent eye movements but synchronize both eyes during saccadic prey tracking. *Exp. Brain Res.* **139**, 173–179. https://doi.org/10.1007/s002210100774 (2001).
26. Gisi, M. J. *Das Gehirn von Hatteria punctata.* Ph.D. Dissertation, Universität Basel, iv + 166 pp + 1 (1907).
27. Paulina-Carabajal, A. *et al.* A look in to the neurocranium of living and extinct Lepidosauria. In *Paleoneurology of Amniotes, New Directions in the Study of Fossil Endocasts* (eds. M. T. Dozo, A Paulina-Carvajal, T.E. Macrini, & S. Walsh) 123–178 (Springer, 2023).
28. Shanklin, W. M. The central nervous system of *Chameleon vulgaris*. *Acta Zool.* **11**, 425–490 (1930).
29. Fischer, J. G. *Die Gehirnnerven der Saurier anatomisch untersucht* (J.A. Meissner, 1852).
30. Diaz, R. E. Jr., Shylo, N. A., Roellig, D., Bronner, M. & Trainor, P. A. Filling in the phylogenetic gaps: Induction, migration, and differentiation of neural crest cells in a squamate reptile, the veiled chameleon. *Dev. Dynam.* **248**, 709–727. https://doi.org/10.1002/dvdy.38 (2019).
31. Gross, J. Ueber die Sehnervenkreuzung bei den Reptilien. *Zool. Jahrb.* **17**, 763–799 (1903).
32. Jeffery, G. PNS features of rodent optic nerve axons. *J. Comp. Neurol.* **366**, 370–378 (1996).
33. Fontana, M. *Traité sur le vénin de la vipere sur les poisons Americains sur le Laurier-Cerise et sur quelques autres poisons vegetaux. On y a joint des observations sur la structure primitive du corps animal. Différentes experiences sur la reproduction des nerfs et la description d'un nouveau canal de l'oeil*, vol 2. (No publisher listed, 1781).
34. Aristotle. *Aristotelis de natura animalium libri novem, de partibus animalium libri quattuor: de generatione animalium libri quin. Interprete Theodoro Gaza* (Iohannes & Gregorius de Gregoriis Frattres, 1492).
35. Newton, I. *Opticks: Or, a treatise of the reflexions, refractions, inflexions and colours of light. Also two treatises of the species and magnitude of curvilinear figures.* [iv] + 144 + 211 + [1], 18 pls. (Sam. Smith, and Benj. Walford, 1704).
36. Perrault, C. *Description anatomique d'un cameleon, d'un castor, d'un dromadaire, d'un ours, et d'une gazelle*. (Frederic Leonard, 1669).
37. Vallisnieri, A. *Istoria del camaleonte affricano, e di varj animali d'Italia*. (Gio. Gabbriello Ertz, 1715).
38. Panaroli, D. *Il Chamaleonte esaminato*. (Francesco Cavalli, 1645).

39. Briggs, W. 3. A continuation of a discourse about vision, with an examination of some late objections against it. *Philos. Trans. R. Soc.* **13**, 171–182 (1683).
40. Tidhar, L.-A. *Visual acuity and visually guided avoidance behavior in the common chameleon (Chamaeleo chameleon)* M. A. thesis, University of Haifa (Israel), viii + 49 pp + 2 (2014).
41. Bennis, M. et al. A quantitative ultrastructural study of the optic nerve of the chameleon. *Brain. Behav. Evol.* **58**, 49–60 (2001).
42. Nava, S. S., Conway, M. A. & Martins, E. P. Divergence of visual motion detection in diurnal geckos that inhabit bright and dark habitats. *Funct. Ecol.* **23**, 794–799. https://doi.org/10.1111/J.1365-2435.2009.01565.X (2009).
43. Fleishman, L. J. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.* **139**, S36–S61. https://doi.org/10.1086/285304 (1992).
44. Regalado, R. Social behavior of dwarf geckos (*Sphaerodactylus*): a comparative repertoire. *Ethol. Ecol. Evol.* **24**, 344–366. https://doi.org/10.1080/03949370.2012.702685 (2012).
45. Hedges, S. B. & Thomas, R. At the lower size limit in amniote vertebrates: a new diminutive lizard from the West Indies. *Caribb. J. Sci.* **37**, 168–173 (2001).
46. Thomas, R. A new gecko from the Virgin Islands. *Q. J. Florida Acad. Sci.* **28**, 117–122 (1965).
47. Röll, B. Gecko vision–retinal organization, foveae and implications for binocular vision. *Vision Res.* **41**, 2043–2056 (2001).
48. Evans, L., Hardtke, F., Corbin, E. & Claes, W. Camouflaged chameleons: a new discovery at the Egyptian site of el-Hosh. *Archael. Antropol. Sci.* **12**, 158. https://doi.org/10.1007/s12520-020-01125-y (2020).
49. Albertus Magnus. *Divi Alberti Magni de animalibus libri vigintisex novissime impressi* (Joannem et Gregorius de Gregoriis, 1495).
50. Pliny the Elder. *Naturalis Historia*. (Spira loannes [Joanis de Spira], 1469).
51. Solinus, C. *Iulii Solini De Situ Orbis Terrarum, et Memorabilibus quæ Mundi Ambitu Continentur, Liber*. (Impressus per Nicolaum lenson Gallicum, 1473).
52. Bennis, M., Repérant, J., Rio, J.-P. & Ward, R. An experimental re-evaluation of the primary visual system of the European chameleon, *Chamaeleo chameleon*. *Brain. Behav. Evol.* **43**, 173–188 (1994).
53. Huber, G. C. & Crosby, E. C. On thalamic and tectal nuclei and fiber paths in the brain of the American alligator. *J. Comp. Neurol.* **40**, 97–227 (1926).
54. Mitra, A. T. et al. Ocular lens morphology is influenced by ecology and metamorphosis in frogs and toads. *Proc. R. Soc. B.* **289**, 20220767. https://doi.org/10.1098/rspb.2022.0767 (2022).
55. Currea, J. P., Sondhi, Y., Kawahara, A. Y. & Theobald, J. Measuring compound eye optics with microscope and microCT images. *Comm. Biol.* **6**, 246. https://doi.org/10.1038/s42003-023-04575-x (2023).
56. Sumner-Rooney, L., Kenny, N. J., Ahmed, F. & Williams, S. T. The utility of micro-computed tomography for the non-destructive study of eye microstructure in snails. *Sci. Rep.* **9**, 15411. https://doi.org/10.1038/s41598-019-51909-z (2019).
57. Sándor, P., Frens, M. & Henn, V. Chameleon eye position obeys Listing's law. *Vis. Res.* **41**, 2245–2251 (2001).
58. Tweed, D. & Vilis, T. Geometric relations of eye position and velocity vectors during saccades. *Vision Res.* **30**, 111–127 (1990).
59. Čerňanský, A. et al. The only complete articulated early Miocene chameleon skull (Rusinga Island, Kenya) suggests an African origin for Madagascar's endemic chameleons. *Sci. Rep.* **10**, 109. https://doi.org/10.1038/s41598-41019-57014-41595 (2020).
60. Bolet, A. & Evans, S. E. In *The Biology of Chameleons* (eds. Tolley K. A. & Herrel A.) 175–192 (University of California Press, 2013).
61. Vidal, N. & Hedges, S. B. The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *C. R. Biol.* **332**, 129–139 (2009).
62. Jones, M. E. et al. Integration of molecules and new fossils supports a Triassic origin for Lepidosauria (lizards, snakes, and tuatara). *BMC Evol. Biol.* **13**, 208 (2013).
63. Kumar, S. et al. TimeTree 5: an expanded resource for species divergence times. *Mol. Biol. Evol.* https://doi.org/10.1093/molbev/msac174 (2022).
64. Sieradzki, A. Designed for darkness—The unique physiology and anatomy of owls. In *Owls—Clever Survivors* (ed. Mikkola, H.) 1–19 (IntechOpen, 2022).
65. Steinbach, M. J. & Money, K. E. Eye movements of the owl. *Vision Res.* **13**, 889–891 (1973).
66. Money, K. E. & Correia, M. J. The vestibular system of the owl. *Comp. Biochem. Physiol. A.* **42**, 353–358 (1972).
67. Krings, M., Nyakatura, J. A., Boumans, M., Fischer, M. S. & Wagner, H. Barn owls maximize head rotations by a combination of yawing and rolling in functionally diverse regions of the neck. *J. Anat.* **231**, 12–22. https://doi.org/10.1111/joa.12616 (2017).
68. Molnar, J. & Watanabe, A. Morphological and functional regionalization of trunk vertebrae as an adaptation for arboreal locomotion in chameleons. *R. Soc. Open. Sci.* **10**, 221509. https://doi.org/10.1098/rsos.221509 (2023).
69. Micheti, E. *Il Camaleonte Anatomizato*. 31 pp., 3 pls. (Gio. Giacomo Komarek, 1699).
70. Schwaner, S. A., Feola, A. J. & Ethier, C. R. Factors affecting optic nerve head biomechanics in a rat model of glaucoma. *J. R. Soc. Interface* **17**, 20190695. https://doi.org/10.1098/rsif.2019.0695 (2020).
71. Beebe, W. New data on the deep sea fish *Stylophthalmus* and *Idiacanthus*. *Science* **78**, 390–390 (1933).
72. Beebe, W. Deep-sea fishes of the Bermuda Oceanographic Expeditions. Family Idiacanthidae. *Zoologica* **16**, 148–241 (1934).
73. Buschbeck, E. K. & Hoy, R. R. The development of a long, coiled, optic nerve in the stalk-eyed fly *Cyrtodiopsis whitei*. *Cell Tissue Res.* **321**, 491–504 (2005).
74. Gignac, P. M. et al. Diffusible iodine-based contrast-enhanced computed tomography (diceCT): an emerging tool for rapid, high-resolution, 3-D imaging of metazoan soft tissues. *J. Anat.* **228**, 889–909. https://doi.org/10.1111/joa.12449 (2016).
75. Blackburn, D. C. et al. Increasing the impact of vertebrate scientific collections through 3D imaging: The openVertebrate (oVert) Thematic Collections Network. *Bioscience* **74**, 169–186. https://doi.org/10.1093/biosci/biad120 (2024).
76. Collin, S. P. et al. Bioimaging of sense organs and the central nervous system in extant fishes and reptiles in situ: A review. *Anat. Rec.* https://doi.org/10.1002/ar.25566 (2024).
77. Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W. & Pyron, R. A. Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biol. Conserv.* **204**, 23–31 (2016).
78. Diaz, R. E. et al. Captive care, raising, and breeding of the veiled chameleon (Chamaeleo calyptratus). *Cold Spring Harb. Protoc.* **2015**, 943–949 (2015).
79. Conroy, C. J., Papenfuss, T., Parker, J., Hahn, N. E. Use of tricaine methanesulfonate (MS222) for euthanasia of reptiles. *J. Am.Assoc. Lab. Animal Sci.* **48**, 28–32 (2009).
80. Jr Diaz, R. E., Bertocchini, F., Trainor P. A. Lifting the veil on reptile embryology: The veiled chameleon (Chamaeleocalyptratus) as a model system to study reptilian development *Meth. Mol. Biol* **1650**, 269–284 (2017).

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Author contributions

The project was conceived by E.C., R.E.D.Jr., E.L.S., and J.D.D. Measurements were taken by E.C., A.H.M., E.L.S. and J.D.D. Visualization of anatomical structures were done by E.C., E.L.S., A.H.M., and J.D.D. Funding was

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